THE GENERIC POSITION OF *OSMUNDITES DOWKERI* CARRUTHERS

BY

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SYNOPSIS

A silicified rhizome from the Thanetian of Herne Bay, Kent, formerly described as *Osmundites dowkeri* Carruthers, is now referred to the sub-genus *Plenasium* of the living *Osmunda*. This has been possible owing to the discovery of another better preserved rhizome in Thanet, coupled with fuller knowledge of the family Osmundaceae. Recent studies by W. Hewitson show clearly characters which distinguish the three living genera and various sub-genera of the Osmundaceae. The fossil material is described in detail. Especial attention is given to the distribution of sclerenchyma in the leaf base and wing stipules. The presence of two protoxylem groups in the leaf traces within the cortex is demonstrated. The form and number of the xylem bundles in the cylinder of the rhizome is displayed. A close affinity with rhizomes described by C. A. Arnold from the Eocene of Clarno, Oregon, is emphasized. A possible connexion between the Thanetian rhizomes and the common Eocene foliage described as *Osmunda lignitum* (Giebel) by Heer and Gardner is suggested in view of the fact that this foliage appears also to belong to *Plenasium*.

INTRODUCTION

THE fossil species *Osmundites dowkeri* Carruthers, based on a single rhizome from the Thanetian of Herne Bay, Kent, has been known since 1870. It has been described or mentioned in several publications but without any full and accurate descriptions of the anatomy. This omission was due in the first place to the fact that the importance of some of these details was not realized but in later works is, in part at least, to be attributed to the poor condition of the solitary specimen hitherto known. The published evidence shows clearly the Osmundaceous characters but no attempt was made previously to establish the true generic position, hence the name *Osmundites*. The particular choice of name may have been dictated originally by the inherent mistrust which some palaeobotanists invariably showed about the use of Recent generic names for incomplete fossil material. Its retention in later work was due to the immense amount of research needed on living genera before relationship with *Todea* and *Leptopteris* could be excluded. Such research of course involved the preparation of many slides from rather intractable material to discover what characters in rhizomes of the different genera were of diagnostic value so that the knowledge could be applied to fossils. This, coupled with the difficulty of obtaining for dissection a sufficiently large range of living forms, has been a stumbling block to further research. But without it no sound opinion on the particular generic affinity of the fossil could be given.

RECENT INCENTIVES TO RESEARCH ON *OSMUNDITES DOWKERI*

The discovery of a better preserved fern rhizome at Herne Bay by D. J. Jenkins (Chandler 1961 : 51, pl. 1, figs. 1, 2) stimulated the desire to determine the generic position of *Osmundites dowkeri* more accurately. Fortunately in 1962 Hewitson published a comprehensive study of the family Osmundaceae demonstrating that even if the rhizomes only are known, *Osmunda* can be distinguished from *Todea* and *Leptopteris*. He further showed the range of characters within the Recent genus *Osmunda* and how these could be applied in separating its three sub-genera, *Osmunda*, *Osmundastrum* and *Plenasium*. Hewitson's research made it clear beyond doubt that the two Thanetian rhizomes not only belong to the same genus and species but to the sub-genus *Plenasium* of *Osmunda* itself. They should therefore henceforward be known as *Osmunda* (sub-genus *Plenasium*) *dowkeri* (Carruthers).

SUMMARY OF PREVIOUS WORK AND GENERAL DESCRIPTION OF MATERIAL

Both known specimens are silicified, the holotype being a large piece of a mature rhizome, whereas the newly found specimen is smaller and younger, apparently representing the subapical region of a young plant or a young branch of a plant. The holotype (V. 29629) has twice been described by Carruthers (1870 : 349, pl. 24, figs. 1–3 ; pl. 25, figs. 1, 3, 4 ; and more briefly 1872 : 52, pl. 2, fig. 8). It was also mentioned by Gardner & Ettinghausen (1880 : 53) and by Seward & Ford (1903 : 254) but these authors made no attempt to redescribe the rhizome or to discuss its affinities in any detail. Kidston & Gywnne-Vaughan (1907 : 768) gave a further account but apart from an excellent description of the diarch roots they added little to what was already known although they did stress the strong curve taken up by the xylem of the leaf trace almost immediately after it has left the stele of the stem. They also gave a diagrammatic transverse section of the wing stipules and leaf base (1907, pl. 6, fig. 5) which they believed provided the only distinctive specific character in Osmundaceous stocks. The fungus infested condition of the tissues and resultant deterioration prevented them from giving any further description of the transverse section which they show in pl. 4, fig. 21. The magnification of this figure is too small to show the really significant features which are also much obscured by partial disorganization both of the specimen and of the slide.

Arnold (1952 : 72), in describing two Osmundaceous rhizomes from the Eocene Clarno Beds of Oregon, referred briefly to *Osmundites dowkeri* because it closely resembled his new species, *Osmundites Chandleri*, in the strong curve of the emergent leaf trace. Nevertheless he stated (p. 75) that the two were so remote geographically and geologically as not to justify even a consideration that they might be the same.

In both Thanetian specimens, as in all Osmundaceae rhizomes, the small true stem is surrounded by a thick mantle of spirally arranged leaf bases which accounts for most of the thickness seen. In neither is evidence of fronds or fructifications preserved. Hewitson (1962 : 88) confirmed Kidston & Gywnne-Vaughan's views as to the importance of the distribution of sclerenchyma in the leaf bases and demonstrated that this character could be used to discriminate between species,

sub-genera and genera. On the evidence of petiole base structure it can be stated definitely therefore that the two Herne Bay specimens are specifically and generically identical despite differences of size and age. The specimen V. 29630 is much better preserved than the original holotype. Added to this the late W. N. Croft prepared from it an exceptionally fine thin section for he was a master craftsman in this as in all such matters. The better preserved material is therefore described here, before considering the detailed characters still visible in the holotype, for it has much to contribute towards the fuller understanding of the larger older rhizome.

DETAILED EXAMINATION OF V.29630

General Considerations.

The rhizome found on the shore at Hampton, Swalecliff, Herne Bay, and like the holotype presumed to come from the Thanetian was figured by Chandler (1961 : 51, pl. 1, figs. 1, 2) to show the gross characters. The maximum length preserved was 53·2 mm. and the diameter 35 × 45 mm. The rhizome broadens slightly upwards the maximum diameter at the lowest point being only about 27 mm. The cross section is elliptical. The outer surface has been abraded to such a degree that the stipes above the stipule wings and the extreme upper ends of these wings have always been removed. The upper surface of the specimen is a deep basin-like depression with rim of unequal height owing to differential breakage and abrasion. The form of this basin is dictated by the angles the stipe bases form with the true stem, about 23°. Such a narrow angle is most nearly approached in the living sub-genus *Osmundastrum* (15°–25°) but this has proved to be very unlike the fossil in other respects. In *Plenasium* the corresponding angle is 30°–45° ; in *Osmunda* (sub-genus) 25°–40° ; in *Todea* and *Leptopteris* about 30° (Hewitson 1962 : 73). The walls of the basin are formed by an amorphous silica casing which must have filtered in solution into the interstices between the silicified petiole bases. As a result the true ventral surfaces of petioles and wing stipules are not exposed except in minute patches where the casing has chipped away. The length and form of the wing stipules cannot therefore be recorded but the 30 mm. depth of the basin with wing stipules still in transverse section on its upper rim indicates that they must have been more than 30 mm. long. The bottom of the basin is formed by pith, xylem cylinder and amorphous silica occupying the space once filled by cortex, this tissue having disappeared. The basin like form of the upper end of the specimen indicates that growing tip and younger leaves had been torn away prior to fossilization leaving the tougher tissues of the somewhat older leaves just below. These leaf remains have become silicified cell by cell around the true stem. A similar basin was seen in *Todea barbara* when tip and youngest fronds were removed. After silicification superficial chemical action appears to have operated differentially in the apical region. The silicified xylem cylinder with protruding roots has been left in relief by etching out most of the inner cortex. The cavities resulting from this etching are now filled by redeposited coarse irregular grains of silica. The silicified leaf traces beyond the outer cortex are structurally intact except that the stout

cylinder of sclerenchyma which delimited each has been dissolved leaving cylindrical or variously distorted hollows. These reproduce the irregular forms of the leaf stipes in section. The siliceous casing which penetrated between the stipes now remains as a complicated upstanding network (Pl. 5, fig. 11). Within the casing are embedded hairs, roots and wing stipules all full of structural detail. The removal of what in the living plant was the strongest and most resistant part of the stipe may be due to incomplete penetration by silica of the dense thick walled sclerenchyma cells. These changes are secondary and purely superficial phenomena for the sclerenchyma cells are perfectly preserved inside the rhizome as shown in a section about half way down the specimen. But even inside the rhizome the parenchyma of the inner cortex has gone, its place being taken in the slide by amorphous silica except in one small patch. The slide (V.29630a) is the outcome of the late W. N. Croft's technical skill and patience. He describes its preparation in his working notes in the following words : " ground one side of slide flat. Treated this with polystyrene with much solvent (benzene) in which alizarin had been ground. Scraped off dried crust with razor blade. Examined surface with binocular after wetting with cedar oil. Staining was fairly satisfactory stain having been taken up by some of the xylem strands, although patchily. Hardening of slice was in any case necessary as it was somewhat porous ".

V.29630 was clearly a relatively young rhizome for its stipes were soft and the wing stipules flexible. Hence the regularity of arrangement seen in the firm older holotype is not present. (cf. description of stipes and wing stipules on p. 146).

Anatomical Structure.

The Pith, about 1·5 to 2 mm. in diameter, is formed of typical parenchyma as seen in transverse section (part only being represented by amorphous silica). The cells are commonly 0·05 to 0·1 mm. in diameter, rarely 0·14 mm. At the circumference of this tissue there are a few rows of cells, varying in number, only about half this size. Some of the larger cells towards the circumference show dark staining. In view of the limited material, no longitudinal section is available.

The Xylem Cylinder and Leaf Traces. The counting of the xylem bundles which form the cylinder has been carried out consistently in all sections examined whether of this or the holotype and in accordance with a plan suggested by Hewitson to secure uniformity of treatment. Without such a plan the number would vary considerably with the personal factor. Hewitson, throughout his research, treated bundles connected by even a single tracheid as one. Otherwise, he explains, "cases are encountered where it is difficult to make a decision ". On this basis there are twenty strands in V.29630a, a large projecting horse-shoe trace being regarded as one although one of its limbs is almost but not quite severed from the arc (Pl. 2, fig. 3 ; Pl. 3, fig. 6). A noticeable feature in the xylem ring is a somewhat oblique horse-shoe on a radius at right angles to the larger horse-shoe above described. It has one limb completely separated (counted separately therefore) the remaining one forming a query-shaped bundle with the hook towards the circumference of the stem (Pl. 3, fig. 6). On the opposite side of the xylem ring (below right) is a query-shaped

pair of bundles with adjacent hooks (Pl. 2, fig. 3 ; Pl. 3, fig. 5). There is also a query-shaped bundle bending to unite with an oval bundle (Pl. 2, fig. 3 at 2 o'clock). Various stages of the development of one of the large horse-shoes from the fusion of two query-shaped ones can be seen in the slide. In addition there are a number of pointed or pointed-oval bundles one or two of which show a tendency to be hooked on account of a slight excavation of the outline on one radial margin.

The development of leaf traces can be admirably seen by comparing slide V.29630*a* (Pl. 2, fig. 3) with the smooth lower surface of V.29630 from which it was cut, this surface representing a slightly higher level in the rhizome (Pl. 4, fig. 7). The largest horse-shoe strand of the slide has separated into two distinct bundles each with a small median notch on its inner side (Pl. 4, fig. 7). A completely separated deeply C-shaped leaf trace formed by the separated apex of the horse-shoe has already passed into the outer cortex. All departing leaf traces have a pronounced C-shape. Within the inner cortex of the slide one leaf trace shows an initial stage of separation. Others are completely detached. The outer limit of the five-sided light coloured inner cortex is easily traced (Pl. 2, fig. 3). Its sides, slightly concave, alternate with sharp angles. They stand out clearly from the darker coloured outer cortex surrounding it and forming the outermost part of the true stem. The outer cortex is in its turn readily distinguished from the leaf sheath by its darker colour and by the delimiting sclerenchyma of the leaf bases seen wherever an included leaf trace projects in any degree at all beyond the cortical tissue (Pl. 1, fig. 2). The structure of the outer cortex appears to be homogeneous with well preserved parenchymatous cells except as stated above where the bounding sclerenchyma of projecting leaf traces is developed externally.

There are two protoxylem groups in all traces within both regions of the cortex. They are visible at the inner angle of each arm of the C-shaped xylem strands (Pl. 2, fig. 3 ; Pl. 4, figs. 8, 9 ; Pl. 5, fig. 10). In thin sections they are not very easy to detect at first because of the blurring resulting from the oblique sections of leaf trace in which the cells themselves are also frequently tilted slightly by the grinding processes. This is more or less inevitable for leaves arising at an angle from the central xylem cylinder are bound to be sectioned somewhat obliquely in a transverse cut across the rhizome axis. In slide V.29630*a* a trace in the outer cortex on the opposite side of the xylem cylinder to the large horse-shoe strand clearly shows one of its protoxylems as a group of about six small cells at the inner angle of one limb (Pl. 2, fig. 4) while the second is seen in a blurred section in a corresponding position on the other limb. By tilting the slide slightly under the microscope a true cross section of a trace in the inner cortex which has just separated from the stele can be observed. It lies adjacent to roots (Pl. 3, fig. 5). By using strong reflected light on the polished solid surface of V.29630 from which the section was cut two protoxylems are more readily apparent under the microscope on traces within the true stem for here the details are not blurred by tilting of the cells (Pl. 4, figs. 7–9). In both xylem strands and leaf traces the position of the protoxylem may further be indicated by a slight elongation and convergence of the adjoining metaxylem strands in transverse section (Pl. 2, fig. 4 ; Pl. 3, fig. 5).

The number of leaf traces in the cortical region is regarded by Hewitson as of some importance. He counts only those traces which are actually free from the stele but whose outer limits, as shown by absence of sclerenchyma ring, do not project beyond the outer cortex (see p. 145). The slide shows four leaf traces in the above restricted sense of which two lie wholly in the outer cortex. For living Osmundaceae Hewitson (1962 : 73) gives the following figures :

Sub-genus *Plenasium* 3 to 8 traces (o to 1 inner cortex ; 3 to 8 outer)

Sub-genus *Osmunda* 8 to 14 traces (2 to 4 inner ; 5 to 11 outer)
   O. lancea is exceptional with 12 to 22 (1 to 5 inner ; 11 to 15 outer)

Sub-genus *Osmundastrum* 11 to 27 traces (4 to 12 inner ; 7 to 15 outer)

Genus *Todea* 6 to 12 traces (2 to 5 innner ; 3 to 8 outer)

Genus *Leptopteris* 4 to 15 traces in small rhizomes in two of the three living species (o to 3 inner ; 3 to 13 outer) 9 to 27 traces (in a large rhizome of *L. superba*) (o to 8 inner ; 4 to 20 outer).

As can be seen the numbers vary in the different genera and sub-genera. The closest to the fossil is *Osmunda* (*Plenasium*) *banksiaefolia* with four traces in the entire cortex but differing in that there are none in the inner cortex and four in the outer.

The Leaf Mantle. Outside the true stem in the leaf mantle, the newly departed leaf bases still show two protoxylem groups with C-shaped or reniform xylem bands (Pl. 1, fig. 2 ; Pl. 2, fig. 4, bottom right). Passing towards the circumference of the rhizome, i.e. in a position equivalent to a higher level on the emerging stipes, the traces develop a broader larger opening on the adaxial side, gradually becoming broader and flatter themselves (Pl. 1, fig. 1). As a result of this development the outermost, oldest, petioles preserved in the mantle have a broad xylem band with incurved ends and wide opening. In these older outer stipes the protoxylem has divided into a number of separate strands which are seen in section lying along the inner concave outline of the xylem band. (Pl. 5, fig. 12 ; Pl. 6, fig. 14, where the strands are just visible in the photographs as deeply stained patches. They are very clearly seen in the slides themselves).

As in all Osmundaceae, petioles which have emerged from the stem are surrounded entirely by a stout thick ring or ellipse of sclerenchyma often about o·14 to o·34 mm. thick (Pl. 5, fig. 12). In the emerging traces still partly embedded in the outer cortex this sclerenchyma belt is obvious only on the protruding outer surface of the petiole as described (Pl. 1, fig. 2). No wing stipules have been preserved on the first two whorls of petioles outside the stem (Pl. 6, fig. 14 below, left) but in subsequent whorls of the loosely arranged and somewhat flexible young stipes the stipules are much twisted and curved. Some stipes are tangentially compressed and radially elongate with much distorted xylem as seen in section (Pl. 6, fig. 14 right), others are narrow and elongate tangentially (Pl. 6, fig. 14 left, above and centre).

On first emerging typical stipe dimensions are as follows, the tangential measurement being given first in every case : 2·55 by 1·14 mm. ; 3·34 by 1·14 mm. ; 3·07

by 0·11 mm. Radially elongate stipes are 2·39 by 2·28 mm. ; 3·07 by 2·28 mm.
At the extreme circumference typical measurements are : 8 by 7 mm. ; 3·5 by
4·2 mm. ; 7 by 2·8 mm. ; 2·5 by 7 mm. One of the largest outermost stipes lies
parallel with the greatest diameter of the elliptical section and has a total breadth of
about 26 mm. of which the wings measure 8 and 9 mm. respectively. The maximum
radial diameter of this leaf base is 4·5 mm. The wing stipules are formed of coarse
celled light brown parenchyma with scattered, distinctly separated, patches of
sclerenchyma as seen in transverse section (representing the cut ends of long scleren-
chyma strands). The patches lie mainly at one level in the wing but are sometimes
seen at different levels where the wing is thickest (Pl. 5, fig. 12 ; Pl. 6, fig. 14).
There may be from six to nine patches in each wing but apparently the number is
variable. Towards the thin lateral extremities of the wings the sclerenchyma
patches diminish progressively in size. Sclerenchyma has also developed within the
stipe itself starting in the young leaf base at the apex of the bay on the adaxial side
of the stele. Initially only a few sclerenchyma cells are seen in this position. How-
ever passing upwards, as the leaf develops, this small patch increases in size and later
divides into three as can be observed in stipes a little further out in the mantle.
Later still when the trace broadens the sclerenchyma forms several partly united
patches lying near the inner curve of the xylem. Towards the circumference of
the section it has again broken up to form distinct separated patches as is clearly
shown in Pl. 5, fig. 12, lowest stipe, and Pl. 6, fig. 14. More sclerenchyma occurs
within the sclerotic ring of the petiole base on both the adaxial and abaxial sides
of the xylem as well as laterally. Many small scattered quite separate patches are
visible (Pl. 5, fig. 12 ; Pl. 6, fig. 14).

SUMMARY OF CHARACTERS WHICH INDICATE RELATIONSHIP WITH
OSMUNDA, SUB-GENUS *PLENASIUM* IN V.29630

The features described above distinguish the specimen unmistakeably from *Todea*
and *Leptopteris* in the light of Hewitson's researches. Moreover certain characters
ally it with *Osmunda* and within that genus with the sub-section *Plenasium*. These
characters are :

The distribution of the sclerenchyma in wing stipules and leaf base.

As described above. The interrupted character of the adaxial sclerenchyma
adjacent to the leaf trace is encountered in the Japanese and Chinese species *Osmunda*
(*Plenasium*) *banksiaefolia* (Presl) Kuhn. The sub-genus *Osmunda* has, in contrast,
a long continuous sclerenchyma band in each wing in two of the Recent species
and in all three (*Osmunda regalis, O. japonica* and *O. lancea*) little or no scattered
sclerenchyma within the continuous sclerenchyma ring, nor is the adaxial scleren-
chyma associated with the leaf trace arranged as in the fossil (cf. Hewitson 1962, fig. 7
A, B, C). In the sub-genus *Osmundastrum* the continuous sclerenchyma ring is very
distinct from that of the fossil in that it is formed of two kinds of sclerenchyma.
Todea, although it has scattered sclerenchyma within the wings and continuous

ring of the stipe, lacks any sclerenchyma on the adaxial side of the leaf trace in Hewitson's material while Kidston & Gywnne-Vaughan (1907, pl. 6, fig. 7) show, diagrammatically, only a very weak and limited development of such sclerenchyma in *Todea barbara*. *Leptopteris* has either a few well developed sclerotic patches in each wing or numerous very poorly developed strands, but within the continuous sclerenchyma ring of the stipe scattered strands are lacking in all species.

The xylem characters.

Especially the two protoxylem groups in the leaf trace prior to its separation from the stem and the query-shaped bundles with hook directed towards the outside in the xylem cylinder. Two protoxylem groups in such positions are normal in all *Plenasium* species in which also, as in the fossil, the xylem trace has a marked C-shape immediately after it departs from the stele. Hewitson records having seen one specimen of *Osmunda regalis* from India with two protoxylem groups but this is a rare condition in the sub-genus *Osmunda*. In view of the other *Plenasium* characters which the fossil shows it seems reasonable to regard its two protoxylems as indications of this sub-genus rather than as an aberrant type of the sub-genus *Osmunda* which in the other respects it does not resemble. The number of xylem bundles (twenty) in the cylinder of the stem is rather high for *Plenasium* which has about three to twelve, the sub-genus *Osmunda* varies from four to eleven, *Osmundastrum* seven to twenty-two, while in the genera *Todea* (two to seven) and *Leptopteris* (three to twelve) low bundle numbers are found with marked confluence of the bundles. From species to species in each sub-genus and genus there is some variation. Thus *Osmunda* (*Plenasium*) *javanicum* has three to eleven, *Osmunda* (*P.*) *vachellii* nine, *Osmunda* (*P.*) *bromeliaefolia* three to twelve and *Osmunda* (*P.*) *banksiaefolia* four to nine. In this respect therefore the fossil is specifically distinct with about twenty to twenty-one entirely separate bundles in the only two specimens seen.

Character of the cortex (Pl. 1, fig. 2).

There is clear separation between the inner and outer cortex and between the outer cortex and leaf mantle due in the latter case to the sharp definition of the sclerenchyma bands on the external surface only of the emerging leaf traces as already described. In *Todea* and *Leptopteris* the outer cortex is of two cell types, the ring around the stipes being thick walled, the remaining tissues of thinner walled cells with larger lumen. In these two genera, therefore, the sclerenchyma ring is clear all round the trace while still within the cortex whereas throughout the whole genus *Osmunda* as shown above it is only apparent where the stipes protrude.

In the fossil there are four traces in the whole cortex (those, that is, whose outer limits as shown by sclerenchyma do not project from the cortex) two of which lie in the inner cortex. The number is determined by the narrowness of this tissue (external diameter of outer cortex 14 by 9·5 mm. and of the inner cortex 5 by 4·5 mm.) combined with the sharp angle of departure of the traces (23°). At its greatest width the outer cortex may be about 3·75 mm. and the inner 0·75 mm. with a least

width of about 0·25 mm. The sub-genus *Osmunda*, and the genera *Todea* and (usually) *Leptopteris* are similar to one another in having up to fifteen traces in the whole cortex while *Osmundastrum* differs even more from V.29630 in having eleven to twenty-seven traces, from four to twelve of these being in the inner cortex which is relatively wide. *Plenasium*, on the other hand, resembles the fossil in the small number of traces (three to eight) with normally nought to one in the inner cortex. However Hewitson stresses that in this respect the point on the rhizome at which the section is taken is important, the number of traces increasing with " an increasing fraction of phyllotaxy and an increasing stem size ", but in *Plenasium* the low number of traces is real, seven traces being the largest number he had seen in a very large rhizome of *Osmunda javanicum* of which one only was in the inner cortex.

RE-EXAMINATION OF THE HOLOTYPE
V.29629, V.29629a and b and slides V.29629c–h and Kidston Collection K.1248

General Considerations.

Having now described and discussed the better preserved specimen it remains to add a few new facts about the holotype and to indicate the reasons for regarding both rhizomes as belonging to a single genus and species.

Carruthers in his original description gave natural size drawings but no dimensions in figures. The specimen when found by Dowker must obviously have been longer than the 110 mm. which now survive, for so many sections have been cut from the central region. These inevitably must have meant the grinding away of an appreciable length. The rhizome is now represented by an upper (V.29629a & b) and a lower (V.29629) portion. The upper part is 47 mm. long, the lower 63 mm. Carruthers' figures (1870, pl. 1, figs. 1, 2) show the two portions to have been 67 and 73 mm. respectively at that time. This means a loss of some 30 mm. of length from the two pieces. It is not clear whether two complete sections made by Carruthers (V.29629c and V.29629h) were cut before his drawings of the hand specimen were made but probably they were, for the thirty missing millimetres would scarcely cover the preparation of these two thick slides, of slides V.29629d–g, and of the Kidston slide also (K.1248, figured Kidston & Gywnne-Vaughan 1907, pl. 4, fig. 21). K.1248 was prepared commercially by F. Krantz in Bonn in or shortly before 1907. The production of three serial peel sections by Walton in 1930 must also have entailed a further slight diminution of the length of the upper fragment, V.29629a & b. V.29629d was formerly V.2432 and was then entered in the Register (in 1889) as presented by "the late Dr. Millar, March, 1888 " (one specimen). V.29629e (formerly V.40193) is a recent purchase, in 1958, which formed part of the Dufty Collection. The two slides V.29629f and g are all that remain of four registered in 1902 as " V.7103 (one specimen) purchased executors of late George Dowker, 1899 " and " V.7104 (three specimens) Sections of *Osmundites Dowkeri* ". The register indicated that the four slides were all part of V.6126 the former registration number of the holotype. There is nothing to indicate whether Dowker's slide, V.7103, was one of the two survivors or whether both of these survivors belonged formerly to V.7104. The two slides were apparently already missing in 1952 when the whole of the *Osmundites dowkeri* material then extant in the Museum was re-registered
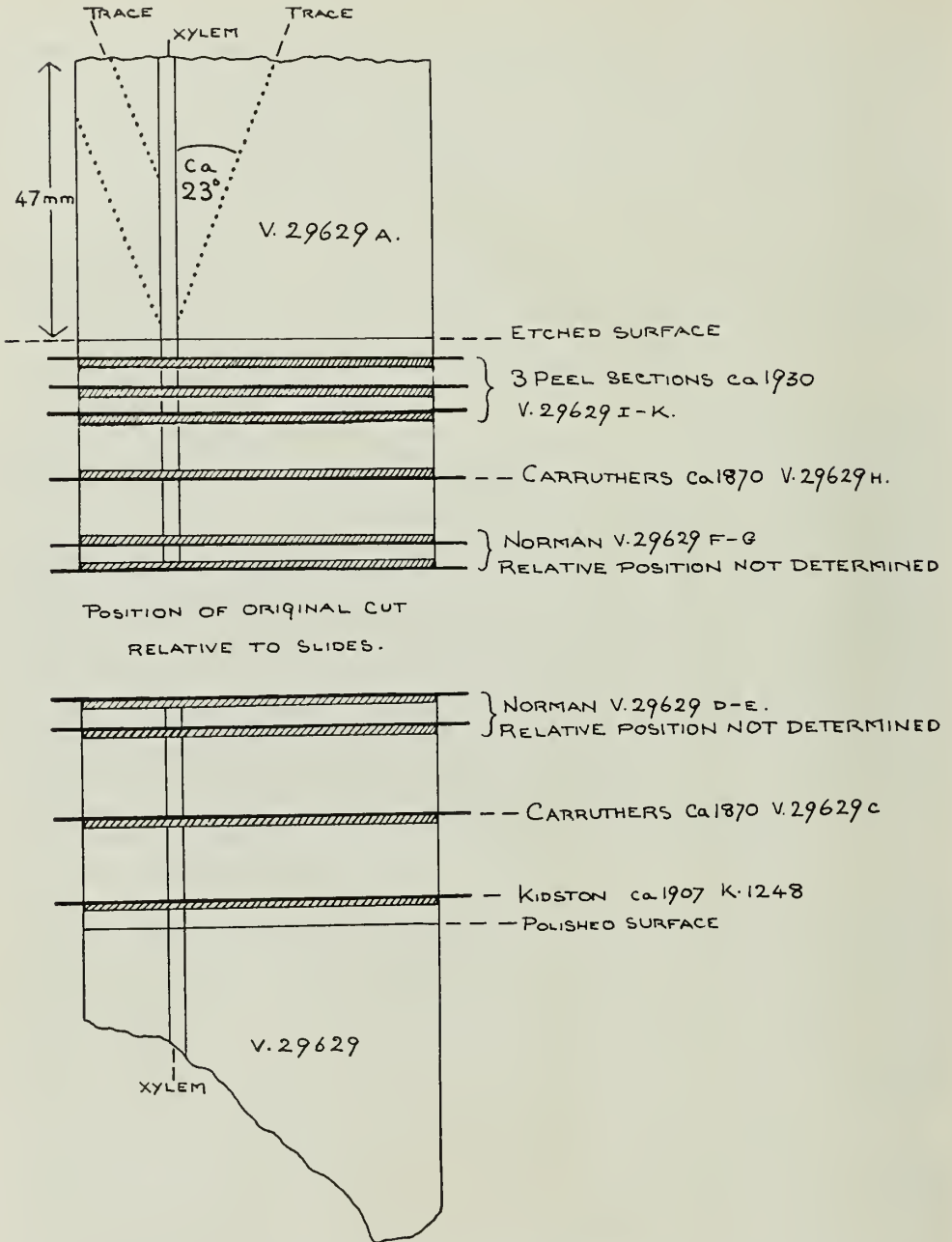
FIG. I.   Diagram showing relative position in rhizome of slides.   For details see text p. 150.
Vertical distances not to scale.   Sections cross hatched.   V.29629*b* is the counterpart
half of the sectioned upper fragment of the rhizome so cannot be shown in the figure.

as V.29629 (seven specimens). One specimen was the hand specimen (then in two fragments) and six were slides which can be accounted for as follows : Two Carruthers slides V.29629*c* and *h* (formerly part of V.6126) ; one peel section now V.29629*k* ; V.29629*d* (see above) and V.29629*f* and *g* (which alone represent the former four specimens V.7103–04).

The slides, V.29629*d*–*g* appear to predate Carruthers' work. They have one feature in common in that all were made by a dealer whose printed label incorporating the words " Norman. Preparator " is on each. Probably the slide from Dowker's executor was one of Norman's. Some of these have been reassembled from other sources (see above). Perhaps the dealer disposed of them in the course of business ; perhaps also of others not traced. This, although irritating, is relatively unimportant in that we now have all the information we need. Of Norman's available slides V.29629*d* is far the best as it includes a good tangential arc of the xylem ring. V.29629*e* is much disorganized. V.29629*f* and *g* are incomplete portions of the transverse section, *f* showing a fragment of xylem ring and mantle on the abraded part of the rhizome and *g* a piece of the leaf mantle from the broad, less abraded side of the stem towards the exterior of the rhizome.

Study of the slides themselves, taken together with a consideration of the foregoing statements, while it cannot give precise distances between the slides shows their former relative positions in the rhizome. These are drawn diagrammatically in Text-fig. 1. Although no record of the sectioning appears to have been kept the sequence of events seems to have been that Dowker, or probably Norman, cut his rhizome in half and slides were prepared professionally by Norman from the two cut ends. The two halves of the hand specimen were then transferred to Carruthers who made two complete transverse sections from the cut ends about 1870. Kidston's section and the peels were the last to be prepared, two of the latter having been acquired in 1963. As a result of the way they were made slides from the upper fragment have the coverslips on the upper side of the slide. Those from the lower fragment must be reversed with the coverslip lying on the underside of the slide in order to place them in correct sequence.

The transverse diameter of the hand specimen V.29629 is 45 by 63 mm. Its leaf mantle is closely compacted. The surface shows the abraded ends of the petiole bases arranged in a steep spiral of about 35° with the axis. As in V.29630 these petioles are always worn away below the upper end of the wing stipules. Consequently neither their transverse sections nor such surfaces as are preserved can show whether the stipules were fused at the apex across the face of the petiole producing a curved commissure. Alternatively they could have persisted as two separate wings one each side of the stipe throughout their length (Text-fig. 2). Kidston & Gywnne-Vaughan (1907 : 766) believed the presence or absence of this commissure to be the only constant superficial distinction between *Todea* stocks on the one hand (including species now assigned to *Leptopteris*) and *Osmunda* on the other, this commissure being found only in *Todea* and *Leptopteris*. Fortunately however it has been shown by Hewitson that there are other cogent anatomical grounds on which the two groups can be distinguished.

Of the hand specimen the lower and upper portion still remain. The upper with its rough unpolished surface has also been sectioned longitudinally into two fragments (V.29629*a* and *b*) but the section runs slightly obliquely passing only in the lower half through the true stem. The grinding processes apparently removed about 6 mm. of the breadth and the pith is only exposed at the lower end of the longitudinal section. The leaf traces are seen to arise from the stem at about 23°, a figure which agrees with that deduced for V.29630. A few details of pith, sclerenchyma, xylem and phloem can be discerned in spite of the difficulty of examining microscopically such dark material by reflected light. Because the material was so limited, no thin longitudinal section was cut. The lower piece (V.29629) of the rhizome is deeply excavated below, only the outer leaf bases remaining at its circumference while the inner leaf bases have been worn in such a manner as to produce the deep conical basal cavity. The upper transversely cut and polished surface of V.29629 lies some 55 mm. above the lowest part of the mantle which forms its circumference. The transverse section shows the true stem to have a diameter of about 13 mm. It lay excentrically in the leaf mantle as the result of abrasion prior to fossilization. Consequently on one side of the specimen all but about two or three layers of the mantle are missing, whereas eight or nine layers are still present along the opposite radius of the rhizome (cf. Kidston & Gywnne-Vaughan, 1907 pl. 4, fig. 21). The least distance between the true stem and the present circumference of the specimen of the more abraded side is only about 5 mm., but along the opposite radius about 34 mm. The original diameter when the rhizome was perfect would have been about 80 to 85 mm. along these radii if abrasion on one side had not been so great. The diameter may well indeed have exceeded the figures suggested for it is probable that some leaf bases may have disappeared from the least abraded side of the rhizome also.

Of the transverse sections which still exist, only six show the whole rhizome. Three of these are valuable peel sections (V.29629*i*, *j*, *k*) which were made very close together at a high level in the rhizome, where the xylem cylinder was less damaged than elsewhere and its tissues were less obscured by fungal hyphae. A comparison of V.29629*j* and *k* shows admirably the changes which have occurred as xylem ring and leaf traces passed upwards (cf. Pl. 8, fig. 16 showing a lower section, V.29629*i*, and Pl. 9, fig. 17). It is regrettable that the section (K.1248) figured by Kidston & Gywnne-Vaughan (1907 : 768, pl. 4, fig. 21) was made at a level where fungal infestation was great and considerable distortion of xylem had occurred, especially on one side, the result of decay combined with radial compression along the shortest diameter. This probably explains why the two authors did not describe the anatomy in greater detail (apart from that of the roots). It also explains the large number of xylem strands which they reported since the partial union of some adjacent strands, now counted as one, is obscured by the radial crushing in this particular section.

Anatomical Structure.

The Pith is about 3·5 mm. in diameter, formed of typical parenchymatous cells frequently about 0·057 mm. in cross section. Around the outer margin there are about six or seven layers, sometimes only three, of somewhat larger cells which appear denser and darker in colour but are shown by the longitudinal section to be normal thin walled equiaxial parenchymatous tissue. In the limited area of pith visible in the longitudinal section no isolated tracheids have been detected but it must be remembered that the section does not pass through the central region of the pith. The pith is continuous with the "rays" of tissue between the xylem strands and no indication of an inner endodermis has been seen.

The Xylem Cylinder and Leaf Traces. The xylem cylinder can be examined in section on the cut surfaces of the rhizome and in seven slides including the peel sections. It is about 4·5 to 5 mm. in diameter and is formed of about twenty or twenty-one entirely separated strands, using again Hewitson's method of counting (cf. p.144). Owing, however, to the radially crushed state of part of the cylinder as explained above the number cannot be seen in most of the available sections for on the side where the crushing occurred it is usually impossible to say whether two adjacent strands are or are not connected as Hewitson specifies " even by one tracheid ". The clearest sections for counting are the peel sections (V.29629*i* and *k*). The xylem strands are separated by some five or six layers of radially elongate parenchyma cells which pass outwards into a parenchyma layer seen in places surrounding the xylem ring. The strands vary much in shape. Two large horse-shoes opening inwards project beyond the outer circumference of the cylinder (Pl. 9, fig. 17). A similar large horse-shoe is seen on the polished lower surface of the upper fragment (V.29629*a*) of the rhizome (Pl. 10, fig. 18). It also shows a leaf trace, just separated from the two arms of a horse-shoe lower down in the rhizome (left in Pl. 9, fig. 17), whose rounded distal end forms the C-shaped trace on this surface. Occasionally traces are elongate at one extremity owing to the initial development of a root (Pl. 9, fig. 17 at 2 o'clock). The origin of a pair of roots is beautifully displayed in peels V.29629*i* (Pl. 8, fig. 16) and *j*. Some adjacent strands are united at their inner ends giving rise to a U or V opening outwards. Such a U is seen to the right of a large horse-shoe (Pl. 9, fig. 17). Two pairs of strands form two adjacent question marks, one reversed, which are well displayed in the peel section V.29629*k* (Pl. 9, fig. 17 top centre, top right). It also shows simple ovals and three slightly united strands forming an S at 6 o'clock. Between the arms of united strands there is parenchyma. Most of the obvious tracheids are large metaxylem elements, smaller ones sometimes occurring at their outer ends. On the walls of the tracheids several lines of narrow pitted or scalariform thickening can be seen.

Some difficulty is encountered in the study of the thin sections because the angle at which the traces spring from the stem again causes transverse sections to cut the leaf traces slightly obliquely. Further the cells themselves may lie slightly obliquely on those slides which are more than one cell thick and in the grinding process some

disorganization of tissues has occurred. For these reasons many of the cell walls have a blurred outline. However, as in the case of V.29630*a*, a slight tilting of the slide in an appropriate direction sometimes clarifies the cell walls. Once again in the holotype a study by reflected light of the opaque polished surfaces of the rhizome itself assists in the understanding of the sections. More especially it is a help in locating the protoxylems for on the solid surfaces distortion and disorganization are at a minimum. Any attempt to reduce further the thickness of the sections might readily lead to worse disorganization. Indeed the thinnest of all, Kidston Collection slide K.1248 is much disrupted. There is good evidence visible on the polished lower surface of the upper fragment (V.29629*a*) of the rhizome close to the remaining small arc of xylem at the longitudinally cut edge (Pl. 10, figs. 18–20). Besides displaying a large horse-shoe trace, it shows V traces opening outwards (Pl. 10, fig. 18) and the initial stages of separation of the rounded end of a horse-shoe to form a trace. In addition there are well preserved completely separated traces in the inner cortex while four are still wholly immersed (in Hewitson's sense) in the outer cortex. Several of these traces offer unmistakeable evidence of small proto-xylem strands at the inner angles of the arms of the C-shaped xylem (Pl. 10, figs. 19, 20) although owing to reflections from the polished surface they are difficult to show by photography. The evidence is best seen if the examination of these solid surfaces is made not by artificial light but in bright daylight without direct sunlight. A low power objective in the microscope shows it clearly. Of the thin slides the evidence most easily seen is in the peels V.29629*i* and *k*.

The successive stages in the development of the leaf trace can be better observed in the holotype than in V.29630 owing to its wider diameter. As the trace passes outwards and upwards the xylem sheath becomes more deeply C-shaped or reniform with only a narrow gap on the adaxial side occupied by about five or six radially elongate cells. This form persists into the outer cortex of the stem. The xylem, by this time horse-shoe shaped with thickened arms, has a metaxylem which may be four or five cells thick within the arms but only about two cells or even a single cell thick at the apex of the horse-shoe. Throughout both regions of the cortex the leaf trace is surrounded by a clear dark line corresponding to the phloem and its associated cells. By the time the trace passes into the outer cortex it may be appreciably larger than it was in the inner. Beyond and surrounding the phloem in the outer cortex there is an oval or ovate belt of thin-walled parenchyma clearly delimited from the normal denser tissue of this region (Pl. 7, fig. 15). The maximum diameter of the inner cortex is about 9 mm., its greatest width from the xylem cylinder to its circumference being about 2 mm. Its outline has seven or eight points separated by slightly concave sides (Pl. 7, fig. 15 ; Pl. 9, fig. 17). The maximum diameter of the outer cortex is about 15 mm. the greatest width between its inner and outer limits being some 3 to 3·5 mm. It also has a seven or eight-rayed outline. Unlike V.29630 the cell structure happens to be well preserved both in the inner and outer cortex (Pl. 9, fig. 17). In this mature rhizome the relatively wide cortex of necessity means that a larger number of leaf traces are sectioned within the true stem than in V.29630. In the entire cortex about ten to twelve completely

immersed traces are visible. In the inner cortex there are six in V.29629*c*, five in V.29629*h–j*, seven in V.29629*k* and five on the polished surface of the lower end of the rhizome (Pl. 7, fig. 15). In the outer cortex there are five in V.29629*c*, *j*, *k* and on the polished surface of V.29629 ; six in V.29629*h*, *i*. That there is a somewhat greater number than in living species of *Plenasium* is no doubt correlated with the greater number of xylem strands in the stem cylinder.

Leaf Mantle. Beyond the true stem for the first four or five whorls the emerged leaves have a more deeply reniform transverse section and then begin to develop a broader larger opening on the adaxial side (Pl. 11, fig. 21). The development of sclerenchyma in the bay of the xylem follows the same course as that described on p. 147 for V.29630. The arrangement of scattered sclerenchyma strands within the continuous ring of the petiole is also similar (Pl. 12, fig. 22 ; Kidston & Gywnne-Vaughan, 1907, pl. 6, fig. 5). The sclerenchyma shows less clearly in the photographs of the thick older slides of the holotype than in the actual slides themselves. It is much clearer in the thinner Kidston slide (cf. wing stipules Pl. 5, fig. 13 ; Pl. 11, fig. 21). The identical character of the leaf bases and wing stipules affords clear evidence that the two rhizome fragments belong to a single species. In contrast to the young stock in V.29630 the leaf bases are tightly and geometrically packed. Kidston & Gywnne-Vaughan (1907 : 769) believed that in close proximity to the true stem the stipules were all concrescent. Since the stipule outlines are perfectly distinct it seems more probable from experience with other fossils that the appearance of concrescence was due to infiltration of silica which later formed a cement. In some newly emerged stipes one wing stipule only may have developed but normally a pair is seen, the stipules here being very short in transverse section (Pl. 12, fig. 23). At this stage the diameter from tip to tip may be only 3·5 to 4·5 mm. and the stipe itself may measure 2·5 mm., the dorsiventral thickness being 2 to 2·75 mm. The stipules broaden laterally upwards as shown in successively older stipes toward the circumference of the mantle but, as stated, in no case is a sufficient length of petiole preserved to show the distal termination of the stipule. This end always appears to have been removed by abrasion. The breadth of the wing stipules is greatest and their dorsiventral thickness least where they lie parallel with the greatest diameter of the rhizome near the circumference (Pl. 11, fig. 21). The largest examples measure 18 mm. in breadth, the actual stipe itself and each wing being about 6 mm., the dorsiventral thickness about 2·75 mm. Midway between the extremes of measurement at the base on the one hand and towards the more distal end of the stipules as preserved on the other there are measurements of about 7 mm. from tip to tip with stipe breadth of 3 mm. and dorsiventral thickness of 2·25 mm. In the highest part of the stipules seen the tips are extremely narrow and may be somewhat curved ; they are presumably less rigid here on account of their thinness. This suggests that little of the distal end is missing so that their total length may not greatly have exceeded 55 mm. A stipule of *Todea* shown in Text-fig. 2 was 45 mm. long which suggests that *Osmunda dowkeri* must have had large stout fronds.

Other Tissues. A sheath of parenchyma surrounds the xylem strands and is thickest in the outer part of the leaf gap, thinnest opposite the strands themselves.
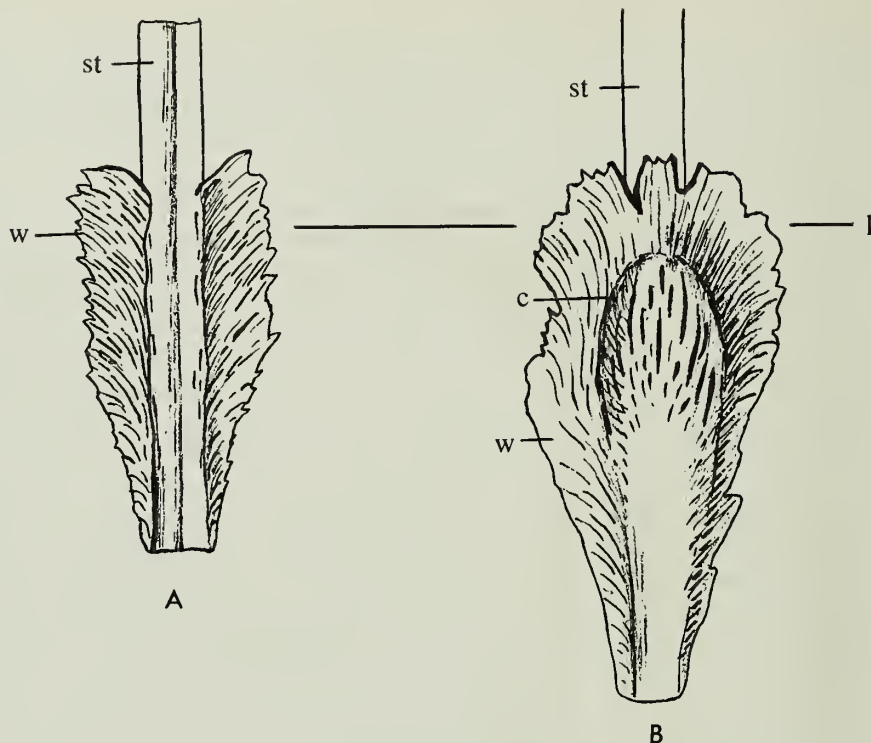
FIG. 2.   Two Recent petiole bases.   A. *Osmunda zeylanica*.   B. *Todea barbara*.

In both the stipe (*st*) flanked by the wing stipules (*w*) but in *Todea* these stipules are fused across the adaxial side of the stipe producing a curved commissure line *c*.   The thick divergent lines and in *Todea* vertical ones below the commissure, indicate sclerenchyma within. Clearly a transverse section at the level *l* in the two cases would appear quite different for in *Todea* the stipules would lie in front of and quite separate from the stipe, whereas in *Osmunda* they would flank it on both sides.   This would be apparent in the section of a fossil stipe at the appropriate level.

Between the xylem strands it constitutes the " medullary rays " of some writers on Osmundaceae.   It is encircled externally by phloem which is followed by tangentially elongate cells.   The large horse-shoes of the incipient leaf traces cause a bulge in the surrounding parenchyma and phloem.   When the leaf traces first appear they are surrounded by a branch of phloem and tangentially elongate cells (much obscured by fungi).

V.29629*d* (Pl. 12, fig. 24) shows very clearly the emergence of a root from one angle of an incipient leaf trace not yet separated from the xylem ring.   Tracheids of the trace can be seen passing directly into the root.   Further evidence as to root development is shown in Pl. 8, fig. 16 ; Pl. 9, fig. 17.

SPECIFIC IDENTITY OF THE TWO SPECIMENS DESCRIBED

It should be noted that the holotype not only agrees with V29630 in the character of the leaf bases of the mantle but also in the two protoxylem strands of traces within the cortex, in the form and number of xylem strands in the stem cylinder and in the deeply curved form of the xylem in the newly separated leaf traces. Hence all lines of evidence point to the specific identity of the two specimens and to their affinity with *Osmunda* rather than with *Todea* or *Leptopteris*. Within the genus *Osmunda* the relationship is with the East Asian sub-genus *Plenasium*.

SIMILARITY TO *OSMUNDITES CHANDLERI* ARNOLD

Only one fossil species resembles the Thanetian *Osmunda dowkeri* at all closely. It is *Osmundites chandleri* Arnold from the Eocene Clarno Beds of Oregon, U.S.A. (Arnold 1952 : 68, pls. 7, 8). In this case the resemblance is so close that in spite of the geographical distance between Oregon and Southern England it cannot be disregarded. Features they possess in common are the presence of two protoxylem strands in the young leaf trace of the inner and outer cortex (well seen by reflected light on the smooth surface of a rhizome kindly supplied by Professor Arnold and perhaps in Arnold's specimen 1952, pl. 7, fig. 12), the C-shaped xylem of the newly emerged leaf, above all the character of the leaf bases both as regards the form of the xylem band and the distribution of sclerenchyma. In *Osmundites chandleri* sclerenchyma within the continuous ring which surrounds the stipe is scattered laterally, adaxially and abaxially. It also occurs on the adaxial side close to the xylem arc and that in the outermost leaves preserved appears to break up into distinct strands as in *Osmunda dowkeri* although a short distance within it is only partially separated into about twelve masses. In the outside whorl of the specimen complete separation had occurred in one or two places and it is possible that larger rhizomes with sufficiently mature stipes would show the same degree of separation that *Osmunda dowkeri* displays (cf. also Arnold 1952, pl. 8, figs. 17, 19). Within the stipule wings of *Osmundites chandleri* the distribution of distinct sclerenchyma patches is identical in the two ; most of the patches are arranged in one line, but they sometimes occur at more than one level. Arnold reports thirty-four oval or horse-shoe shaped xylem strands in the stem cylinder (cf. Kidston & Gywnne-Vaughan thirty). If Hewitson's method of counting were adopted a reduction in this number could be expected but it is not possible from the published figure to make an accurate count as the focus of the print does not show whether any of the strands are partially united. Arnold's pl. 8, fig. 5 shows a half cylinder in which there appear to be about eleven distinct strands. The rhizome received does not clarify this point as the cylinder has broken down on one side. No clear and unmistakeable query-shaped strands could be seen in this specimen although a tendency for the development of this form may be indicated where two bundles turn to one another. Some approximation to this form is seen in Arnold's pl. 7, fig. 13 below the left-hand limb of the just separated trace. See also his pl. 8, fig. 15. Large projecting horse-shoes are a conspicuous feature of the xylem ring. Arnold himself did not press the possible relationship of *Osmunda dowkeri* and *Osmundites chandleri* although he commented on the resemblance

between them. He considered that the geological and geographical separation of the sites from which they came was too great to allow of relationship. It must be borne in mind that distance in these senses does not always exclude specific identity for as Scott (1954) has already shown and is to show still further (unpublished work), identical extinct genera and even identical species do occur among the fruits and seeds of the Eocene Clarno Beds of Oregon and the London Clay of England. As regards difference of age it is now clear that the Lower Tertiary flora persisted at least from the beginning of the Tertiary period into the Oligocene. Should the re-examination of material of *Osmundites chandleri* confirm the suggested relationship to *Osmunda dowkeri* then the former should be referred to Carruthers' species. In any case it seems reasonably certain that *Osmundites chandleri* should be transferred to the living *Osmunda* and to the sub-genus *Plenasium* within it.

A POSSIBLE CONNEXION BETWEEN *OSMUNDA (PLENASIUM) DOWKERI* AND *OSMUNDA (PLENASIUM) LIGNITUM*

It is natural at this point to enquire what evidence there is as to the relationship of the foliage described as *Osmunda lignitum* (Giebel) with living sub-genera of *Osmunda*. The species is represented by beautiful impressions in the Bournemouth Marine Beds (Gardner & Ettinghausen 1880 : 49, pl. 4, figs. 1–3 ; 1882 : 66) and by much broken coriaceous remains in the Bovey Tracey Lignite of Devon (Heer 1862 : 1068, pl. 55, figs. 4–6 ; pl. 56, figs. 1–11 ; pl. 57, figs. 1–7) as well as in numerous Oligocene horizons on the Continent.

In a letter dated 3.8.60 Dr. R. E. Holttum drew attention to the strong resemblance between *Osmunda lignitum* and the Japanese and Chinese species *Osmunda banksiae-folia*. This species, he added, had been included in *Osmunda javanicum* in *Synopsis Filicium* (Hk. & Bak.) although probably distinct. Various species included at one time in *O. javanicum* are closely related forms belonging to the sub-genus *Plenasium*. Gardner & Ettingshausen (1880 : 53) had already noticed the close resemblance between this fossil foliage and " *Osmunda javanicum* " which ranged, they noted, from Kamschatka to Java and Ceylon. At a later date in a Revision of Eocene Ferns for which Gardner alone was apparently responsible (Gardner & Ettingshausen 1882 : 66), the variations of the " species " *Osmunda javanicum* in the different latitudinal areas of its range are described. The statement there occurs that, " It is in the more average-sized pinnae from Formosa, latitude 24° that we meet with the most absolute identity, as far as the fragments admit of comparison, with our fossil forms ".

Additional support for the view that *O. lignitum* belongs to the sub-genus *Plena-sium* is provided in Hewitson's (1962 : 61, text-figs. 1–4) account and figures of foliage in the Osmundaceae. While there is general agreement that the species of *Plenasium* are in need of reappraisal, it is certain that *Osmunda lignitum* has its closest affinities within this sub-genus. Thus the species *Osmunda javanicum*, *O. vachellii*, *O. bromeliaefolia* and *O. banksiaefolia*, discussed by Hewitson, are all characterized, as is *O. lignitum*, by once-pinnate fronds. The sub-genus *Osmunda*

is excluded from close relationship on account of its bipinnate foliage. (Within it Hewitson includes *Osmunda lancea* because it, too, is bipinnate.) His description of the nervation of this sub-genus shows that it is unlike that of the fossil *Osmunda lignitum*. The American sub-genus *Osmundastrum* (*Osmundastrum cinnamomea* and *O. claytoniana*) although it has once-pinnate fronds is distinguished from *Osmunda lignitum* by the deeply dissected pinnae. In *Plenasium*, whatever the ultimate renaming of its species, there is some variation of the margin in the pinnae. It is entire in *Osmunda vachellii* ; entire or toothed in *O. javanicum* ; toothed with narrow pinnae in *O. bromeliaefolia* ; coarsely toothed with wider pinnae as in the fossil in *O. banksiaefolia* where the resemblance is very close indeed. In *Osmunda lignitum* the lateral nerves sometimes give off a greater number of forked tertiary nerves, five or six being shown by Heer on the lower side of the lateral (secondary) nerve (1862, pl. 57, figs. 1, 4), while in the text he mentions as many as seven or eight. In his other figures, however, (cf. Heer 1862, pl. 57, fig. 5 for example) there is complete agreement with Hewitson's text-fig. 41 of *Osmunda banksiaefolia*. In the upper part of the pinnule nearer the tip, *O. lignitum* shows fewer nerves which close to the tip may be undivided. Again in *O. lignitum*, the lowest tertiary nerves are markedly curved and enter the sinus between adjacent teeth where sometimes they unite (Heer 1862, pl. 57, fig. 2). Although most of the tertiary nerves actually spring from a secondary, occasionally a forking nerve arises from a primary one where it passes directly to the sinus (Heer 1862, pl. 6, figs. 1–5 ; cf. Hewitson 1962 : 65, text-fig. 41). The coriaceous character of the pinnules in itself and quite apart from a different nervation, serves to distinguish *O. lignitum* from any species of the filmy ferns *Leptopteris*. *Todea*, too, is quite unlike *O. lignitum* in that its fronds are bipinnate while the lateral nerves of the pinnules have a simple fork or may be unbranched.

The existence of *Plenasium* in the Lower Tertiary of Western Europe on this entirely independent evidence provided by the foliage, demonstrates at least that there is no phytogeographical reason why the rhizomes should not be referred to that sub-genus of *Osmunda*. It further raises the question whether the rhizomes and the foliage belong to a single Lower Tertiary species, having regard to the wide distribution in space and time of many Tertiary plants. There is no direct evidence in support of such a connexion and probably such will never be forthcoming but the possibility must be borne in mind. Should the relationship ever be established, then the specific name *dowkeri* would have to give place to the earlier designation *lignitum*.

SUMMARY OF CONCLUSIONS AS TO THE RELATIONSHIP OF *OSMUNDA DOWKERI* TO LIVING OSMUNDACEAE

The Thanetian species, *Osmunda dowkeri* (Carruthers), now represented by two rhizomes, belongs to *Osmunda*, not to *Todea* or *Leptopteris*. This is shown : (1) By the homogeneity of the sclerenchyma in the outer cortex around the traces and their accompanying parenchyma which causes the sclerenchyma ring of the leaf trace to be apparent only on the abaxial side where the trace bulges beyond the limits of the cortex and true stem (see p. 147).

(2) By the form and distribution of sclerenchyma in the wing stipules of the leaf base combined with the distribution of sclerenchyma in the continuous ring of the emerged stipe and the arrangement of sclerenchyma in the bay of its C-shaped xylem (cf. Hewitson 1962, Text-fig. 7A–M).

Within the genus *Osmunda* in the broad sense, relationship of the fossil is with the section or sub-genus *Plenasium*. This is also demonstrated (1) By the sclerenchyma distribution (again cf. Hewitson 1962, text-fig. 7A–I). (2) By the deeply curved C-shaped form of the leaf trace as soon as it separates from the xylem cylinder. (3) By the presence of a pair of protoxylem strands at the inner angles of the C-shaped traces in the inner and outer cortex. (4) By the presence of query-shaped strands in the xylem cylinder (p. 144). (5) By the low number of leaf traces within the cortex (p. 148).

Osmunda (*Plenasium*) *dowkeri* is distinguished from any living species of *Plenasium* by the greater number of xylem strands in the stem cylinder (twenty or twenty-one approximately) and by the narrow angle at which its stipes emerge (23°).

The possible specific identity of *Osmundites chandleri* Arnold which should also be referred to *Osmunda*, sub-genus *Plenasium*, cannot be lightly dismissed.

The relationship of the Bournemouth and Bovey Tracey foliage of *Osmunda lignitum* (Giebel) to *Plenasium* is clear (p. 158). The possibility that it may be the foliage of the species *Osmunda* (*Plenasium*) *dowkeri*, known only from its rhizomes, must be borne in mind having regard to the long range in time and space of many members of the older Tertiary flora.

The presence of *Plenasium* in the Lower Tertiary of Western Europe, based on independent foliar evidence supports the determination of the rhizomes as *Plenasium*. The finding of this East Asiatic fern genus accords with the phytogeographical indications provided by many Angiosperm families in older Tertiary deposits.

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PLATE 1

Fig. 1. Complete transverse section across rootstock showing central xylem cylinder and limits of outer cortex of stem (dark with angular outline). It also shows the variable form of distorted young leaf bases in surrounding mantle (contrast Kidston & Gywnne-Vaughan 1907, pl. 4, fig. 21). × 3. (slide V.29630a.)

Fig. 2 Central area of above showing dark outer cortex enclosing seven leaf traces, two only completely immersed. A thick sclerenchyma band is seen on outer margins of five traces which abut on edge of cortex. Inner cortex a narrow lighter region around xylem (represented by amorphous silica) enclosing two distinct traces and a third (on left) in process of separating from xylem. A complete ring of sclerenchyma surrounds fully separated traces. × 10.

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PLATE 1

1

2
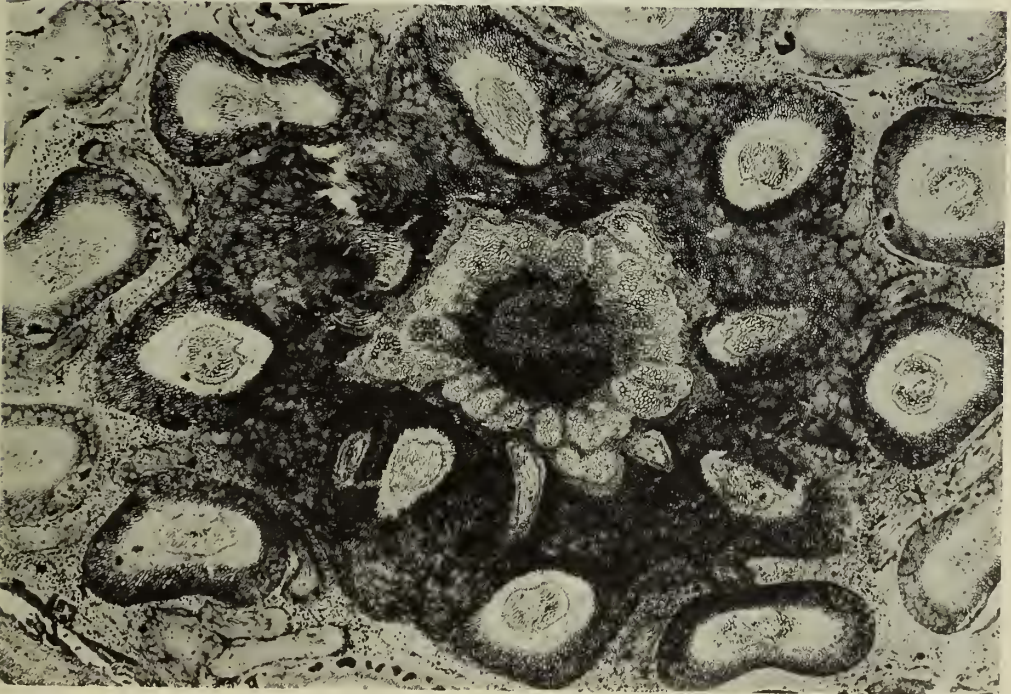
PLATE 2

Fig. 3.   Same as Pl. 1, central area with xylem cylinder and part of cortical region.   Leaf traces on margin of cortex are bounded externally by thick sclerenchyma.   Separating trace (left) has arisen from a horse-shoe trace at a slightly lower level in the rhizome.   A pair of query-shaped xylem strands are seen below (right, at 4 o'clock).   Others are present in upper hemisphere of cylinder.   Two traces which have just separated from it still lie in the inner cortex (below, and on right above).   × 15.   (V.29630a).

Fig. 4.   Right arc of xylem cylinder in Fig. 3 showing query-shaped bundle (below and above) in which position of protoxylem is indicated by convergence of metaxylem tracheids. C-shaped trace in outer cortex (centre) shows one group of small protoxylem cells (inner surface of lower limb of C).   The corresponding group on the other limb is ill preserved.   A newly emerged stipe (slightly out of focus, right corner below) has two protoxylem groups discernable by their deeper staining and greater density due to their small cavities as compared with the metaxylem tracheids.   × 30.
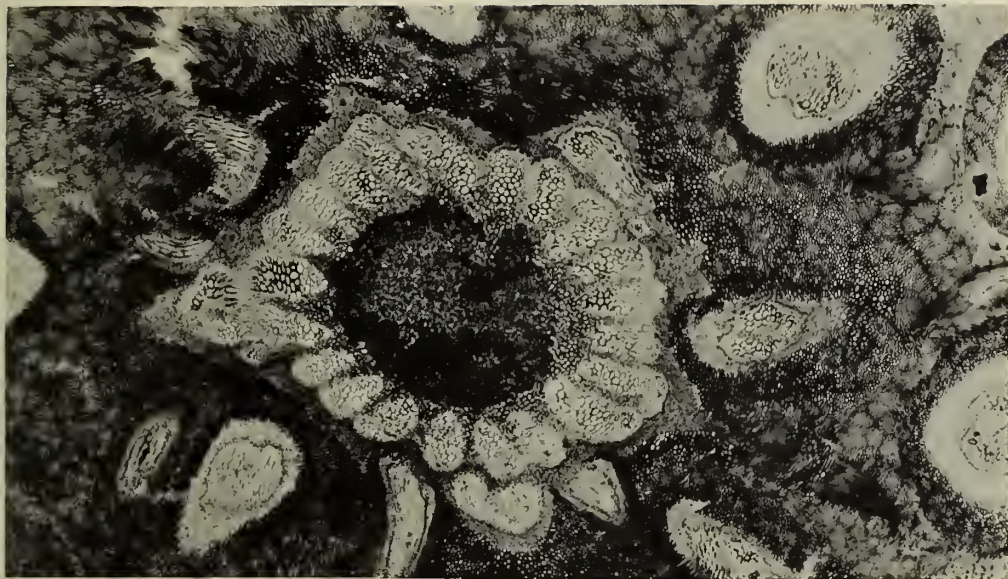
PLATE 2

3
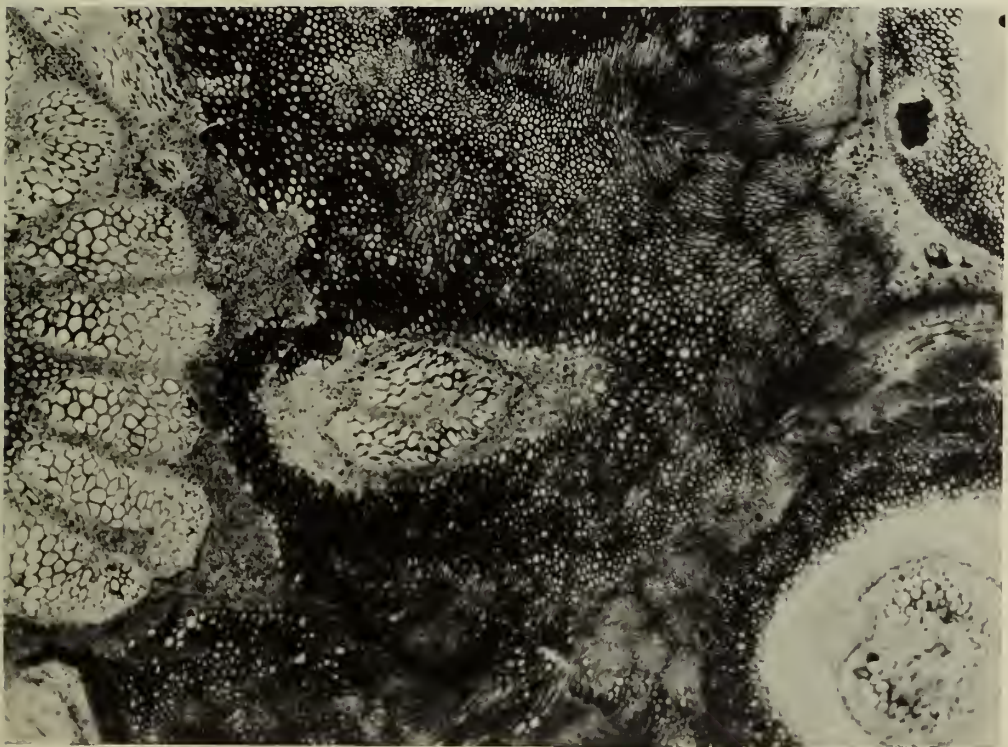
4

PLATE 3

FIG. 5. A trace which has just emerged from lower part of cylinder (cf. Pl. 2, fig. 3) flanked by two roots. Lack of cell structure in inner cortex is clearly due to secondary solution of silicified cells. Some radial distortion of xylem bundles (prior to fossilization) is seen on the left. Pith cells visible on right. × 30. (V.29630*a*).

FIG. 6. The departing trace on the left (cf. Pl. 2, fig. 3). One limb is still attached to the xylem cylinder. The other is severed except for a few tracheids. By comparing the three preceding figures of the xylem cylinder it will be seen that there are at most twenty separate strands (not united by any tracheid). × 30.

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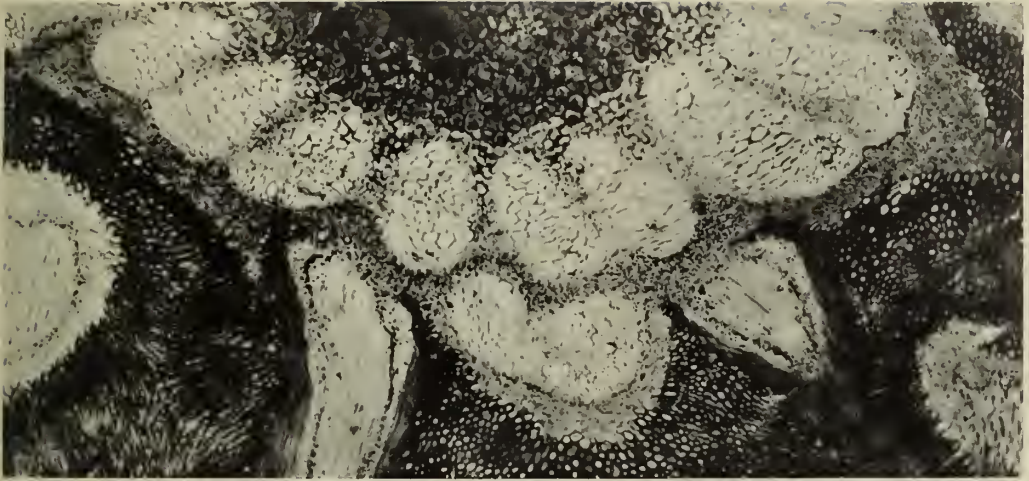
PLATE 3

5
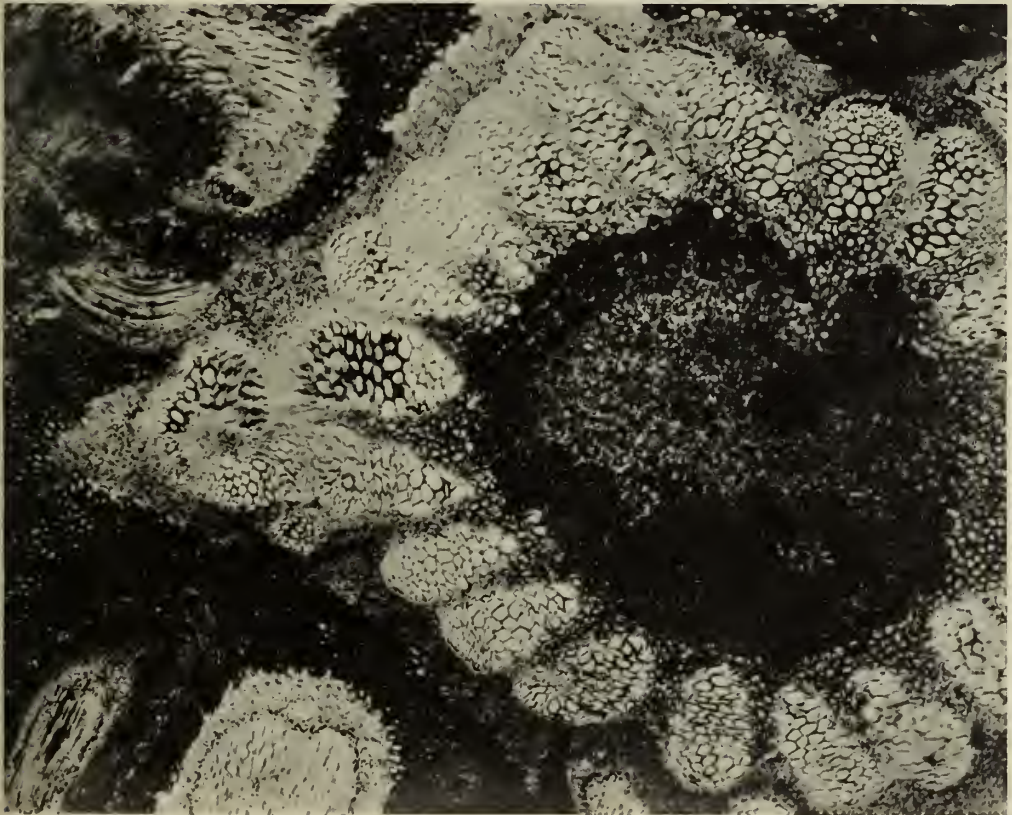
6

PLATE 4

FIG. 7.   Hand specimen from which slide V.29630*a* was cut ; lower surface representing a slightly higher level in rhizome than the slide (cf. Pl. 2, fig. 3).   The departing trace on left is here completely severed. The disrupted trace above was represented by a bulge in xylem of slide (V.29630*a*).   The trace (above, right) has here assumed its deep C-shaped curve.   It was still flattened and lay closely adjacent to xylem in Pl. 2, fig. 3.   The trace (centre right) has now formed its sclerenchyma ring on its outer edge as a preliminary to emerging from stem.   In these traces the slender tracheids of the protoxylem show as dense white patches on inside of limbs of the C.   Various changes in form of individual xylem strands have occurred as can be seen on comparing with the slide (Pl. 2, fig. 3).   × 15.   (V.29630.)

FIGS. 8, 9.   Show traces in surface shown in Fig. 7. The clusters of small tracheids of the paired protoxylem strands are clear on inner angles of the C-shaped metaxylem.   × 30. (V.29630)
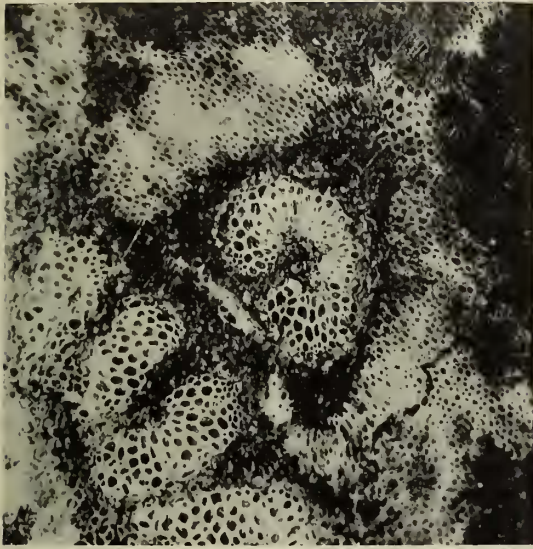
PLATE 4

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PLATE 5

FIG. 10. Leaf trace still within outer cortex but about to emerge as shown by the limiting sclerenchyma on abaxial surface (see base of Pl. 1, fig. 2). Obliquity of section and distortion of cells causes blurring of tracheids but the pair of stained protoxylem strands show as two dark patches on inner side of arms of C-shaped metaxylem in both figures. × 30. (slide V.29630*a*.)

FIG. 11. Basin-shaped upper surface of hand specimen (see p. 143). One large protuberant horse-shoe shaped strand in white xylem ring is visible (top left). Black rings represent hollows formed by solution of silicified sclerenchyma surrounding free stipes. The dark star-shaped outline is due to solution of sclerenchyma which bounds the emerging edges of the traces within cortex. × 6·5. (V.29630.)

FIG. 12. Lower left quadrant of slide in Pl. 1, fig. 1 showing variously distorted stipes each with its complete sclerenchyma ring flanked by sectioned wing stipules. These latter are of loose-textured tissue strengthened by sclerenchyma strands seen in sections as black patches. Sclerenchyma also lies adjacent to inner surface of the xylem arcs. In outer stipes the sclerenchyma has separated into discrete patches. Small patches of scattered sclerenchyma occur throughout the bay of the xylem arc and between the arc and the continuous sclerenchyma ring around its stipe. *oc*, indicates an angle of the outer cortex otherwise cut off by upper edge of photograph. The first two whorls of stipes outside the cortex have suffered some solution of their silicified cells, the space formerly occupied by wing stipules now filled with amorphous silica. × 10. (V.29630*a*.)
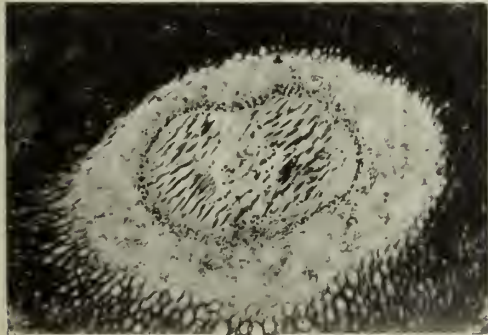
FIG. 13. Two wing stipules from the holotype (Kidston slide K.1248) for comparison with Fig. 12. They show the similar arrangement of the sclerenchyma. × 10.
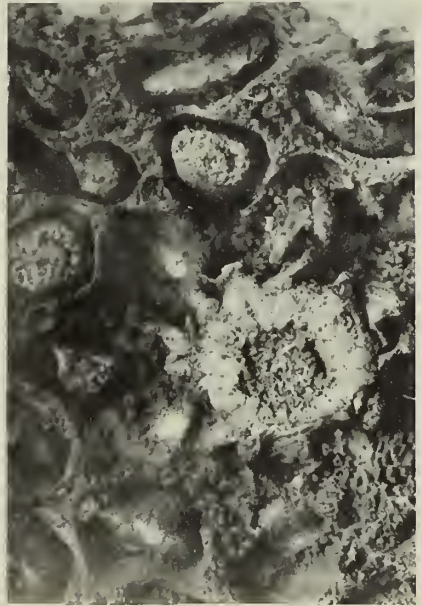
12

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10

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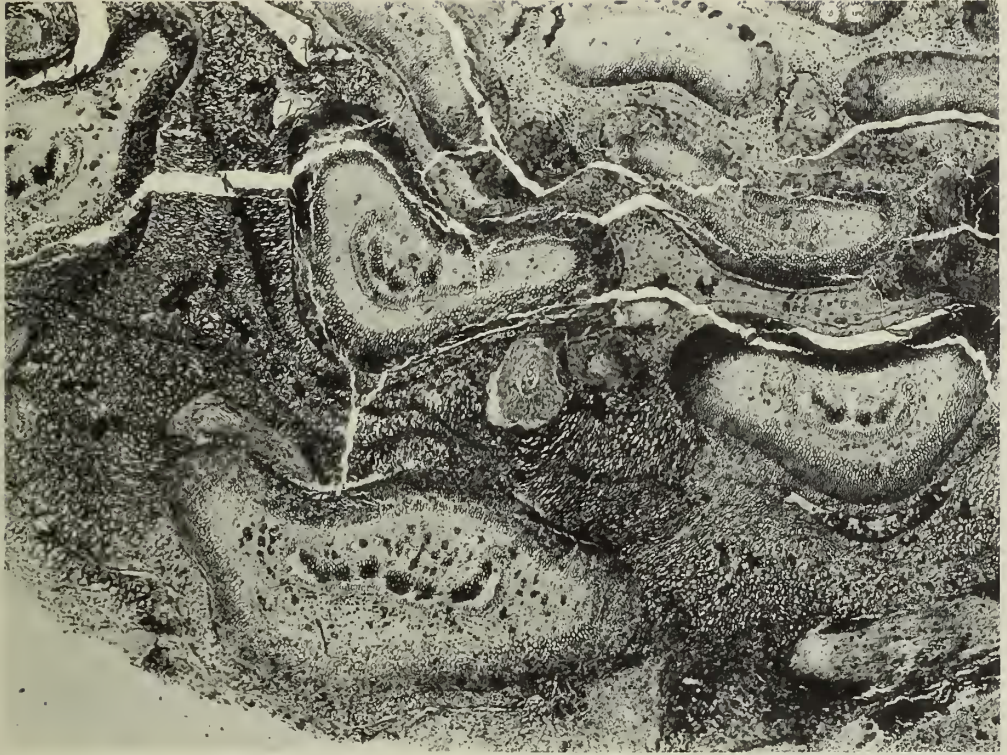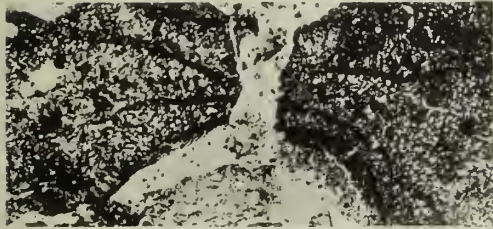
FIG. 14.   View from side of plate.   Upper part of slide in Pl. 1, fig. 1 showing great width of wing stipules which lie parallel with greatest breadth of rhizome.   A stipule is clearly seen to right of uppermost stipe in the figure.   Sclerenchyma in wings and stipe as described in Fig. 12.   × 10.   (V.29630*a*.)

PLATE 6

FIG. 15. View from side of plate (adjacent to most abraded side of rhizome). Central region of holotype as preserved in the hand specimen V.29629 (polished upper surface). The strands of the xylem ring were all much distorted radially before fossilization. Cells of the light coloured angular inner cortex are well preserved in this specimen (cf. Pl. 9, fig. 17; Pl. 10, figs. 18–20; Pl. 12, fig. 24). There are five traces in the inner cortex, one still in close proximity to the xylem (top centre) appearing as a low bulge. The angular outer cortex encloses thirteen traces (only five completely immersed). × 9. (V.29629.)

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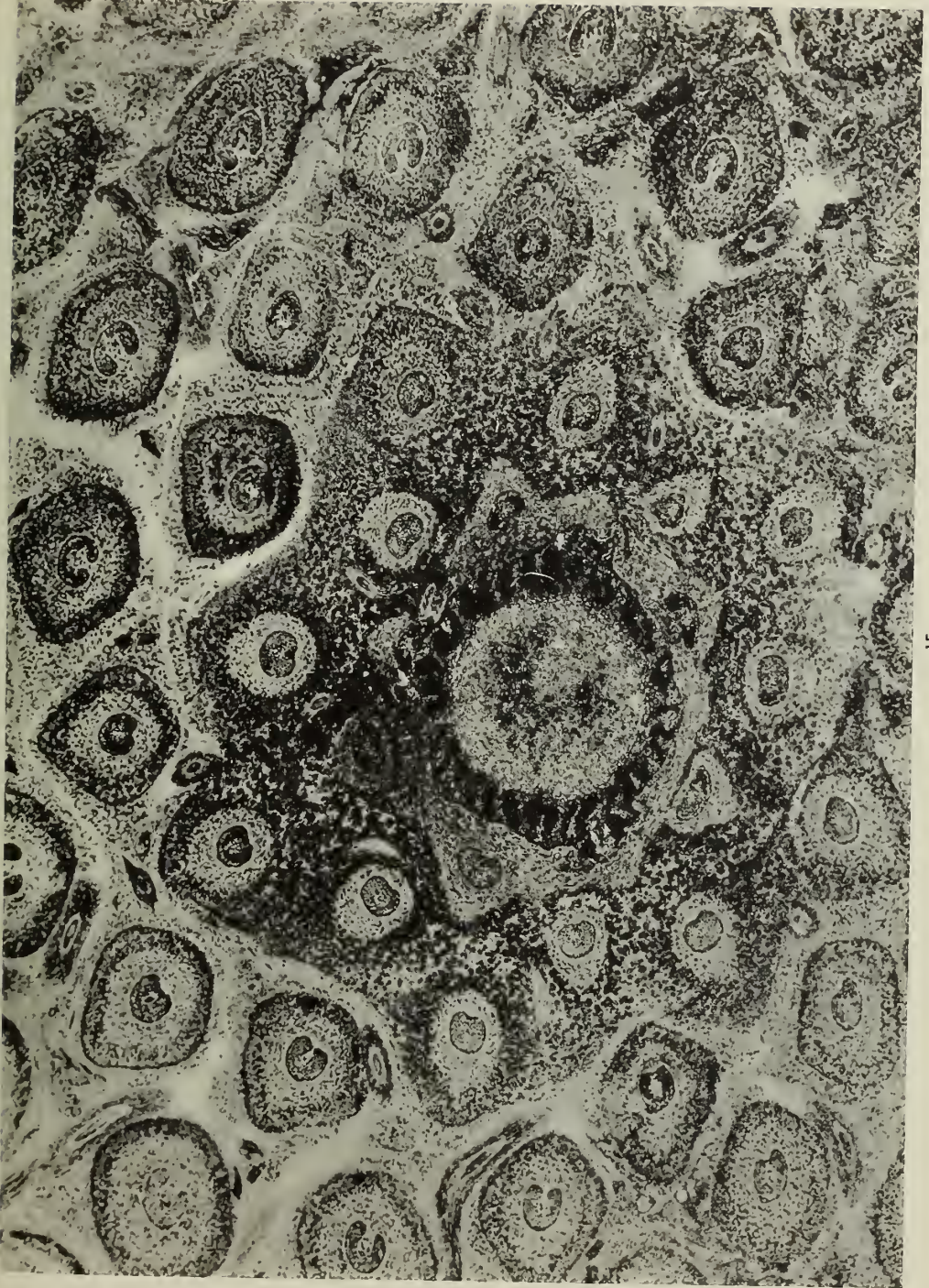
PLATE 7

FIG. 16. View from side of plate (adjacent to more abraded side of rhizome). Centre of a peel section showing xylem ring and surrounding tissues in best preserved region of holotype. There are two large horse-shoe shaped strands (centre base and top left). On the centre left of xylem ring is a departing C-shaped trace from which two roots arise at proximal end of the arms. $\times 15$. (V.29629*i*.) V.29629*j* is a better peel but for technical reasons it gave an unsatisfactory photograph.

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PLATE 8

16
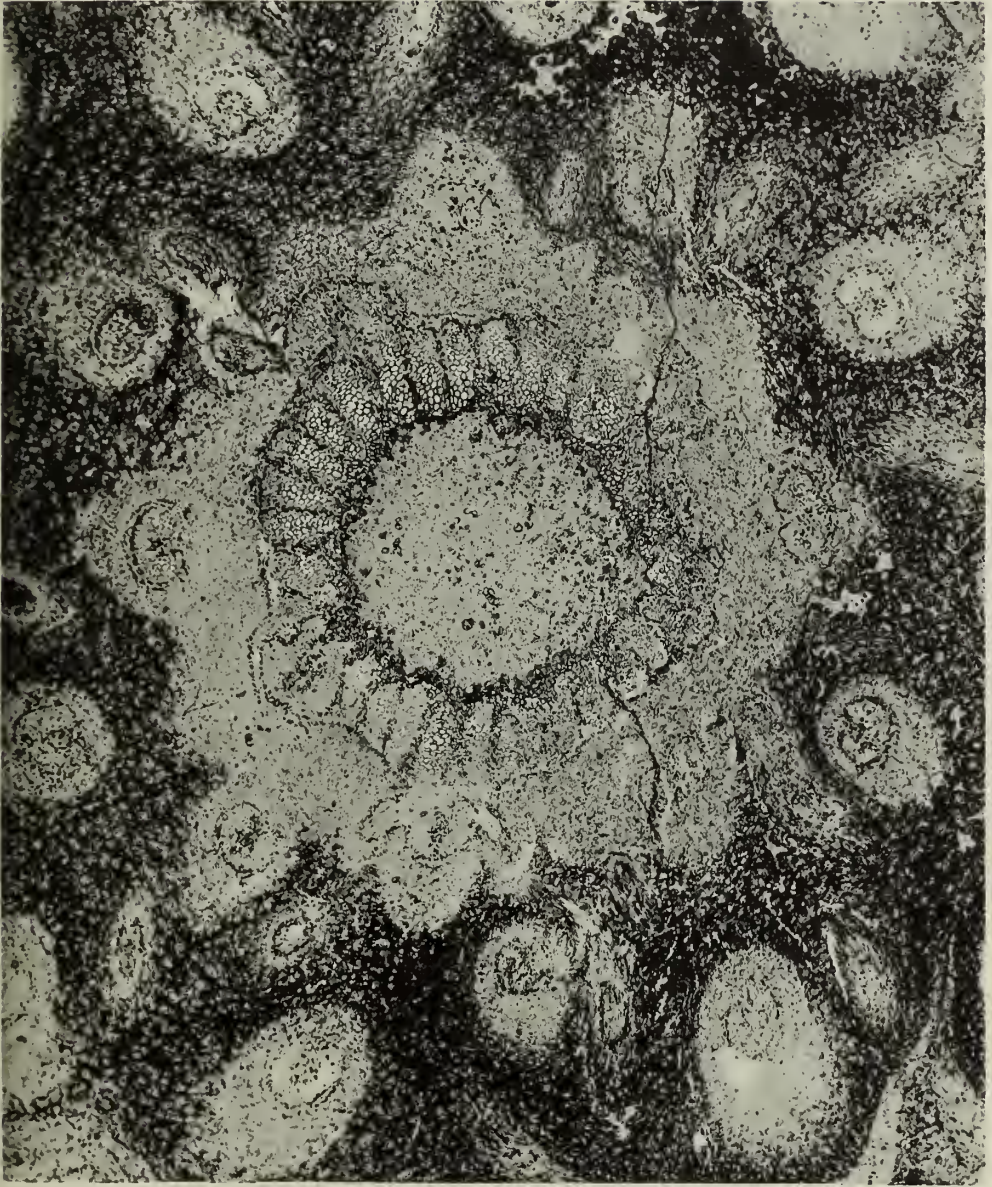
PLATE 9

Fig. 17. View from side of plate as above. Similar region of a peel section taken slightly higher up the rhizome than the preceeding. It therefore shows further development of xylem strands and leaf traces. The same two large horse-shoe strands are seen. There are query-shaped strands (especially top centre and top right), that at top centre united to form central horse-shoe in Pl. 10, fig. 18, also U-shaped strands opening outwards (right at 2 o'clock and top centre), and U-shaped strands opening inwards (left centre). Twenty-one strands of the ring are quite unconnected. Inner cortical tissues are well preserved. Seven leaf traces are seen in the inner cortex. Departing trace with its flanking roots is on the left but the roots are now separated from the trace. (Contrast Pl. 8, fig. 16.) ×15. (V.29629*k*.)
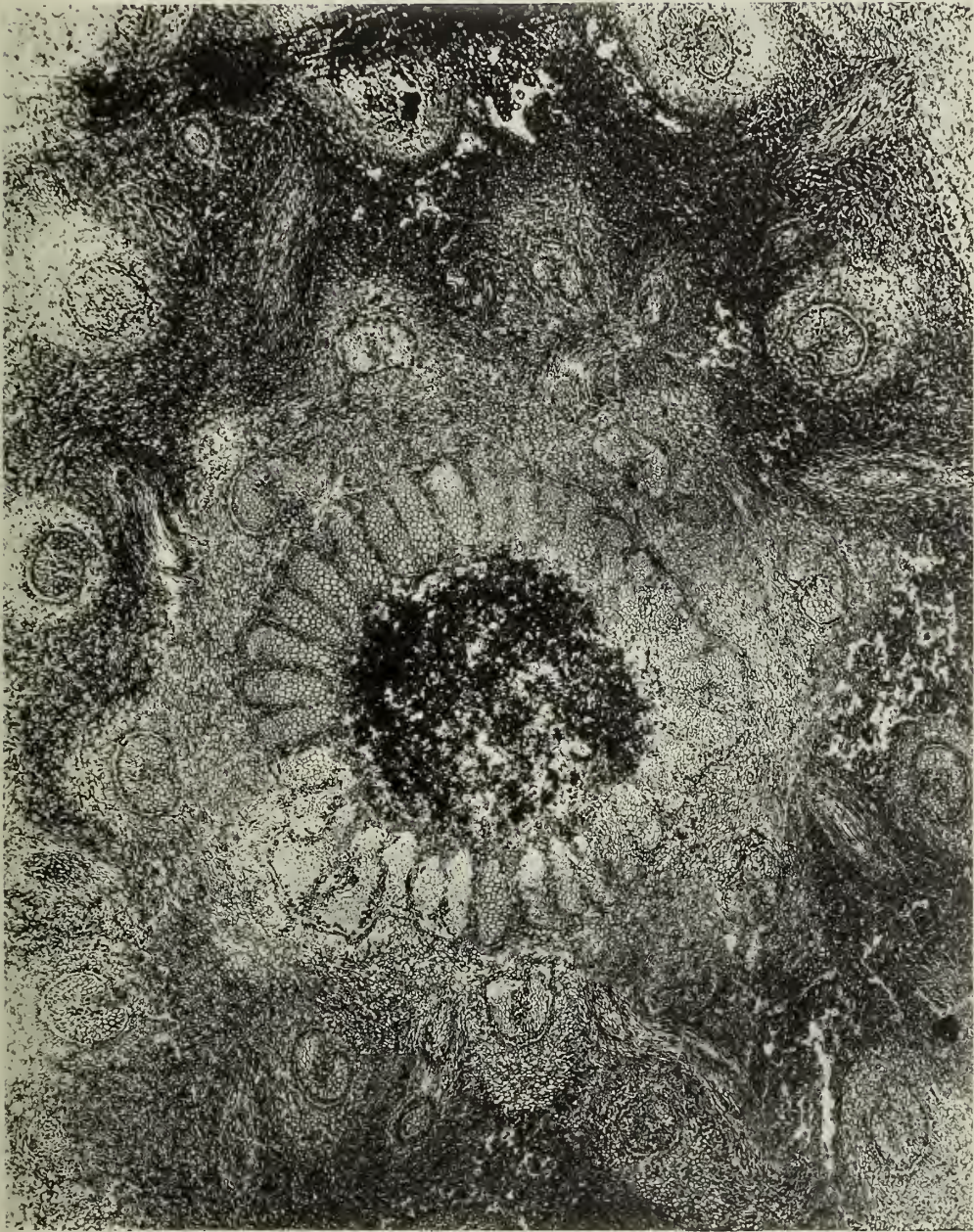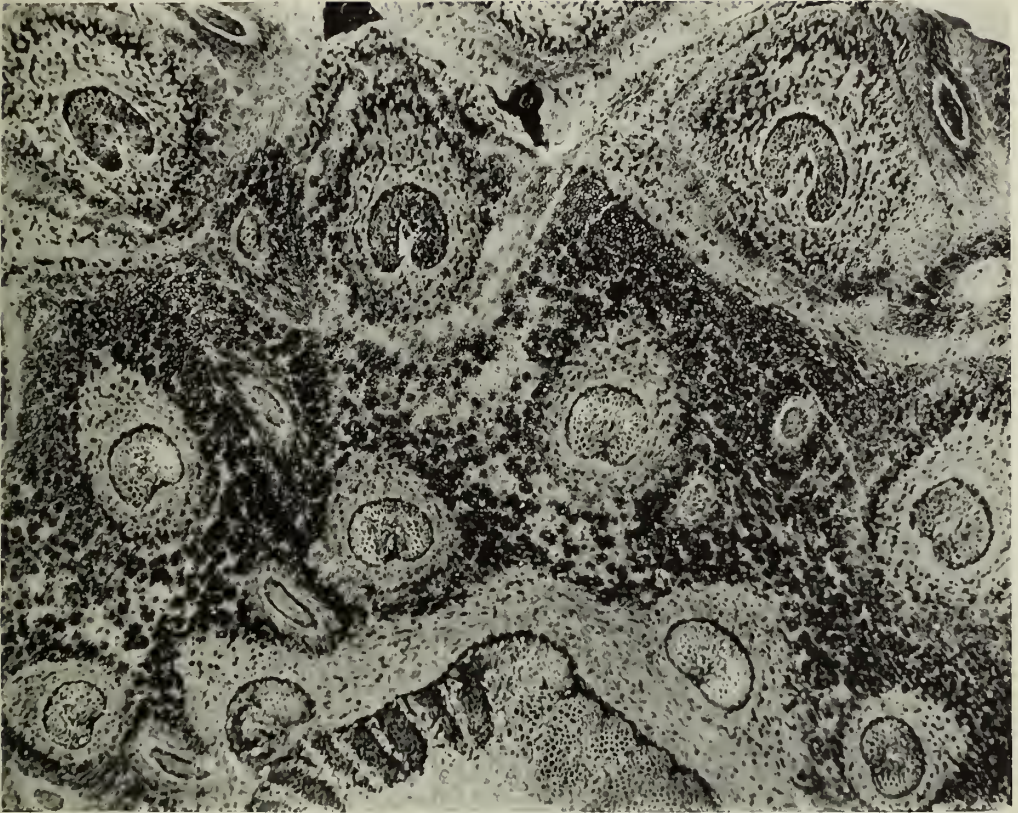
PLATE 9

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PLATE 10

Fig. 18.   Hand specimen (abraded side of rhizome towards top right of figure cf. Pl. 8, fig. 16). Part of xylem ring on polished lower surface of fragment V.29629a.   It shows a horse-shoe strand united to an outward opening U-shaped strand.   There is another outward opening strand on the left.   The trace just departed on left is still connected at lower level of fig. 17 to form large horse-shoe at top left.   A segment of the two cortexes shows C-shaped traces. Innermost layer of free stipes with very short triangular stipules (as seen in section).   × 15.

Fig. 19.   Separated trace in inner cortex of same surface.   Paired protoxylems can be seen by focussing in the specimen but are partly masked by reflections from polished surface in photograph.   On left (base) is U-shaped strand of xylem cylinder opening outwards.   × 30.

Fig. 20.   Another trace on same surface (right base in Fig. 18) which has just passed into the outer cortex.   It is surrounded by an area of thin parenchyma like that of inner cortex.   One of the pair of protoxylems is visible on lower limb, inner surface.   It is very clear on actual specimen.   The other is clearly indicated in the figure in corresponding position on upper limb by elongation and convergence of metaxylem tracheids.   × 30.

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PLATE 10

18

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PLATE 11
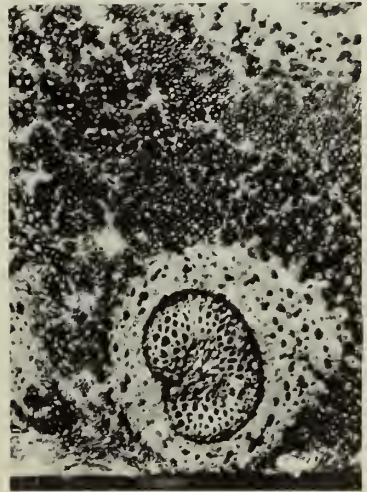
Fig. 21. View from side of plate. Slide showing above the very long wing stipules on broader side of rhizome where leaf mantle thickest. They become shorter towards the true stem and almost non-existent in its immediate neighbourhood at base of figure. Outer cortex cut out by edge of print at base of figure. Sclerenchyma seen in stipule wings as dark patches in outer stipes but patches decrease in number and size passing inwards. Small scattered patches of sclerenchyma show inside sclerenchyma ring in some stipes. $\times 8.5$. (V.29629h.)
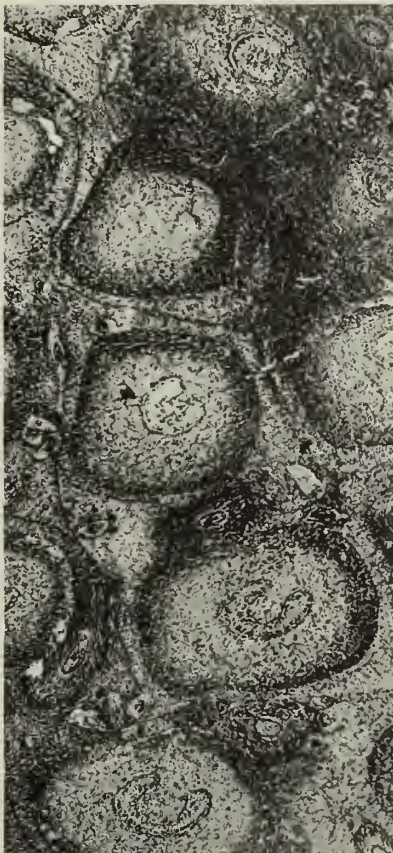
PLATE 11

PLATE 12

FIG. 22.   View from side of plate.   Short wing stipules on more abraded side of rhizome, third row of stipes outside cortex.   Scattered sclerenchyma in sclerenchyma rings seen on left. × 10.   (V.29629*d*.)

FIG. 23.   Stipes on more abraded side of rhizome adjacent to outer cortex with short wing stipules and sparse sclerenchyma.   × 10.   (Peel section, V.29629*h*.)
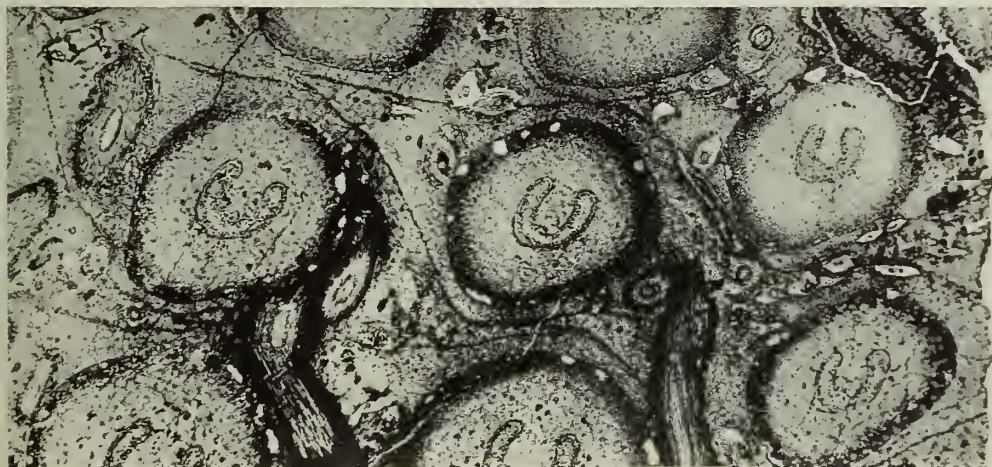
FIG. 24.   Slide showing an arc of xylem with emerging root and trace on abraded side of rhizome.   × 15.   (V.29629*d*.)

PLATE 12